THE MOLLUSCA AS MATERIAL FOR GENETIC RESEARCH.

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In the following pages I wish to comment upon some of the observations and experiments which have been made upon Mollusca that are of importance in the study of genetics. The advantage of such a survey, limited as it is to one group of animals, may not be apparent at first sight. The phenomena of segregation are now known to be almost universal among animals; but it will be, nevertheless, of advantage to know whether certain groups show peculiar types of segregation; whether there are special problems to be studied in certain groups; and whether a special technique is required for certain cases. Co-operation between the taxonomist and geneticist should thus prove to be of advantage.

The prominence given by authoritative workers to the selection hypothesis and to the discovery of unit characters and segregation has had the unfortunate result of making the average naturalist consider that these questions are settled one way or another, or, as an alternative, that both may be true. The phenomena of segregation and unit characters are almost universal, the number of instances of well-attested selective death-rates and the clear demonstration of natural selection at work are very few; yet some of the arguments adduced in favour of the latter hypothesis remain unrefuted, and many phenomena of heredity are only brought under a Mendelian interpretation by dint of considerable straining. There is room, therefore, for more work of an experimental character and great need for field naturalists to carry out supplementary observations according to systematic plans.

At first sight the Mollusca should be a highly satisfactory group for experiment. The shell is a sensitive index of genetic change, albeit susceptible to "fluctuating" variation. It is a permanent and easily visible source of reference. Furthermore, there are certain internal structures (the radula, the dart and jaws of Pulmonata, the mandibles of certain Prosobranchs, and the stomachal plates of Opisthobranchs), which afford admirable material for correlation with the shell characters. On the other hand, they are not quick-breeding animals, the land forms do not have very extensive families, and, though otherwise well suited for study, by reason of their monœcious sex, peculiar copulatory habits, and the tendency among some to bury their eggs, are animals in which the business of exact affiliation is a troublesome matter. We have lastly to consider in detail a question raised by Lang's original work (12) [1] upon Helicidæ. In his first report upon crosses of *H. nemoralis* and

[1] Numbers in ( ) refer to the bibliography at the end of the paper.

hortensis the latter considered that he had showed that self-fertilization did not occur. He found, however, that snails separated after copulation could reproduce themselves, even if *isolated* for three years. He considered this was due to the persistence of the spermotozoa derived from the original copulation in the vesicula seminalis for that period. In a later work (13), however, he announced that a probable case of self-fertilization had been observed ; and Künkel (11) stated that he had actually observed the process. There appears to be very little reason for doubting these observations, which, if they are finally endorsed, should be of great importance in the study of genetics. The question of delayed fertilization is, however, not finally disposed of ; and it is just possible that certain anomalous cases such as those recorded by Stelfox (16) and Collinge (5) may be due to this.

The amount of experimental work done upon Mollusca that satisfies the conditions of an orthodox genetic study is relatively small. A great many observations recorded by Pelseneer (15), some of them adduced by him as evidence against Mendelian heredity, have been made that in one way or another fail to fulfil these conditions. Uncertainty as to the actual parentage, failure to carry the experiments to the F_2 generation and other factors all combine to render these observations, otherwise of value, nugatory as evidence for or against the occurrence of segregation.

The experiments of Lang (12, 13, etc.), supplemented by Kleiner's work (10), and cytological studies by Baltzer (1), are the most important genetic researches upon Mollusca. Of almost equal importance are the results of Stelfox (16, 17) ; while that of Künkel (11) upon *Arion*, though less extensive, deserves mention. The earlier work of Collinge (5), criticized and given a Mendelian interpretation by Cockerell (4), is also worthy of notice.

It is impossible to give a detailed criticism of all this work. On the whole one would say that it affords ample evidence of the presence of unit characters, and segregation. There are several instances, however, in which the meaning of anomalous ratios is not clear, and the interpretation given by authors is not altogether satisfactory. For example, I venture to think that Lang's (13, p. 255) explanation of the proportions of pale-coloured banding in the F_1 and F_2 generations from (P) pale-banded × pale-banded *H. hortensis* is not as satisfactory as some other interpretations of modified F_1 and F_2 ratios.

If the question were to be asked point-blank, " Do these results endorse the geneticist's point of view or do they suggest that some other mode of inheritance is operative ? " I think the answer would be that in such cases as have been carefully worked out the evidence favours the former hypothesis. If there are difficulties of interpretation, the subsequent history of such crosses does not in any case favour the earlier conception of the nature of intermediates.

In this context we may touch very briefly upon Pelseneer's criticisms (15). This is not a very welcome task, as all students of the Mollusca will unite in recognizing their indebtedness to the celebrated Belgian malacologist. But I cannot refrain from expressing the opinion that Professor Pelseneer has failed to exercise discrimination in his review of this subject. He adduces many cases which he considers are not conformable to the concept of unit characters and segregation. For reasons given above, however, the observations cited by him are not admissible as evidence. Furthermore, Professor Pelseneer appears to pin his faith to the F_2 3 : 1 ratio as evidence, and to disregard the well-known modifications of that formula. Again, he is scornful as to certain interpretations based upon imperfect dominance which he ranks among "complications verbales". Now imperfect dominance is a great deal more than this, when one considers how well its action may be tested; and, even if it may not explain all the cases of intermediacy, it cannot be lightly dismissed.

Much might be said on the wide subject of the correlation of the facts of adaptation, distribution, habits, and association with any theory of evolution. The geneticist's point of view has been well stated on this subject by Bateson (2), who draws *inter alia* upon the facts recorded by Coutagne in his account of the polymorphism of the Mollusca of France (6a). The distributional studies of Mayer (14), Gulick (9), Crampton (7) afford little evidence for the orthodox selectionist; and as far as Mollusca are concerned the evidence for a selective death-rate seems to consist only of Weldon's earlier work upon *Clausilia* (18). His later observations (19) were, however, negative. Other cases less well worked out (Boycott (3), Colton (6)) have been put on record, but these are scarcely conclusive. Although the phenomena of adaptation are apparent everywhere in the animal kingdom, it must be confessed that insufficient intensive study has been devoted to the adaptive significance of *specific* characters among the Mollusca. It is an incredible fact that since the publication of "The Origin of Species" sixty years have elapsed without a general concurrence of opinion on this subject being arrived at. And yet every naturalist must be familiar with numerous cases where it is hard to find an adaptive explanation of specific characters other than the customary appeal to ignorance. There is room in the study of the Mollusca for a great deal of observation and intensive study of this question. It cannot be settled without a wealth of observations made in the field upon habits, ecology, food, enemies, etc., and in such matters the general biologist awaits the verdict of the field naturalist. It has been said time after time, but is as true to-day as it was forty years ago, that our knowledge of animal ecology and habits lags far behind our descriptive taxonomy. This balance should be redressed. The experimental side of genetics,

as of any other concept of evolution, must be reinforced by field observations planned in advance to satisfy the many questions in which they may be employed as evidence. Why is a certain variety of *Helix nemoralis* found in locality A and never in locality B ? Do its specific characters appear to be of advantage to it or not ? Do the other snails in locality A tend to show analogous characters or are they different ? If they are different, in what respect are they different ? Do intermediates occur ? If so, what are the offspring of the latter like when they can be bred from known parentage ? These and similar questions the field naturalist should always be asking himself ; and his note-book should be a treasury of information upon food, soil, enemies, habits, and other bionomic data.

Field observations are particularly needful in a special group of cases which in a general way are of considerable importance in genetic studies. Every malacologist has at one time or another been puzzled by certain groups in which structural modifications of an exuberant or bizarre form have been developed. For example, among the Lamellibranchia *Malleus*, *Brechites*, *Tridacna* (e.g. *T. squamosus*), and *Spondylus* are genera in which *bizarrerie* of form or sculpture reaches a maximum. Among Gastropoda *Murex* and *Delphinula* have a fantastic exuberance of spines, certain apparently closely allied species of *Ennea* show a prolific variety of oral armature, while *Opisthostoma* and *Anostoma* exhibit a remarkable abnormality hitherto unexplained. Some of these cases seem to transcend the limits of functional adaptation and to illustrate the principle of momentum discussed by Dendy (8), and attributed provisionally by him to the failure or elimination of growth-controlling secretions. Others seem either to be adapted to very exceptional bionomic conditions or to have become subject to non-adaptive influences diverging very abruptly and eccentrically from the main tendencies of their groups.

Now some sort of adaptive explanation of such cases may be forthcoming. But an investigation in the field is most urgently needed. The elaborate spines of the various species of *Murex*, for example, are at present only explained on an assumption that they are " protective ". If that is the case, what is the enemy that evokes such an elaborate defence absent from some species of the genus and from allied groups ? Are the spines " protective " as a barbed-wire entanglement or do they serve to entangle seaweed and bottom débris so as to impart some sort of " protective resemblance " ? Or can no such factor of special danger be discovered in the environment ? Is it " momentum " or the result of some non-adaptive factorial change ? We cannot dogmatize on such matters. They constitute a lacuna in our knowledge, and a complete and satisfactory account of evolutionary processes cannot be obtained while such cases remain unexplained.

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